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STUDIES ON THE BREEDING CYCLES  
OF  
TROPICAL BIRDS COLLECTED AT 5° SOUTH LATITUDE

By

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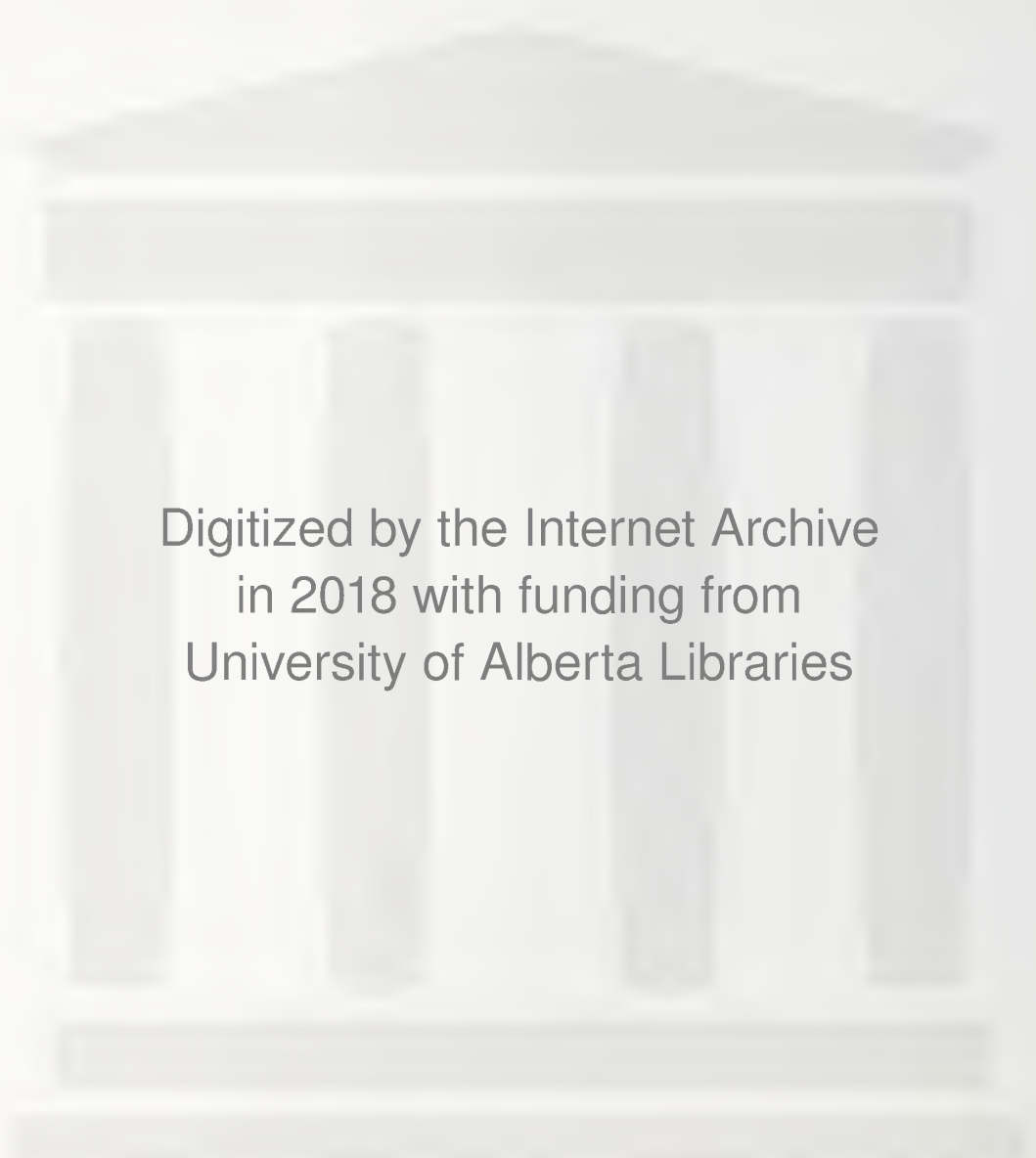
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A Thesis submitted in Candidacy  
for the Degree of Master of Science

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University of Alberta

March, 1942



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## INTRODUCTION

An unfortunate incident, in the fall of 1940, deprived the Department of Zoology at the University of Alberta of its material for proposed experimental studies on the migration of birds, when most of the crows captured for the experiments escaped. It had been previously arranged that I was to take charge of the experiments under Dr. Rowan's supervision and to assist in the histological examination of the gonads. Through Dr. Rowan's generosity, I was able to continue my work for a master's degree when he kindly allowed me to work on some African material that had been sent to Edmonton for histological examination in connection with the studies of breeding cycles in African tropical birds.

Since Rowan (1925) first demonstrated the possibility of manipulating the reproductive cycle of birds through his experimental work on the junco, numerous experiments, on a variety of animal forms, have been performed in several different countries. However, most of the work was done on non-tropical forms of the Northern Hemisphere, where the daylength has been proven to be one of the major controlling factors in the breeding cycles of many birds and animals. Of recent years British investigators (Moreau and Baker) have been working on the



breeding cycles of tropical birds, which they found had definite but extended breeding periods in areas adjacent to the equator, where variations in daylength were practically negligible.

At Amani, Tanganyika, where the material used in this investigation was collected, one finds a most equable climate. An account of the birds of this district have been published by Moreau (1936) from observations extending over a number of years. On Dr. Rowan's suggestion, Moreau agreed to collect a continuous series of gonads of common local species throughout the year for histological examination as a contribution to the study of the timing mechanism in the breeding cycles of tropical birds.

In this thesis I have undertaken to describe, with the aid of charts, graphs and plates, the normal histological changes occurring in the gonads of the species chosen for study, with brief references to the environmental factors and their possible effects on the breeding cycles.

## MATERIAL

The material used in this study was collected by R. E. Moreau during the years 1938-1939 at the East



African Agricultural Research Station at Amani, Tanganyika and was sent to the University of Alberta for microscopical study.

For the study of the yearly breeding cycles of typical Amani nesting species, two specimens of each of three species were collected every fortnight throughout the year; the choice was guided in part by their local abundance. The birds finally selected for study were: -

Colius striatus mombassicus von Someren, a member of the family Coliidae, termed mouse-birds from their creeping habits. The colies are small, tough-skinned birds, which would appear larger were it not for their short, dense feathering. They possess a stout, finch-like bill and a flat, cartilaginous tongue with horny papillae.

Colies frequent forest districts, especially where the brush is thick. They are active, and yet not shy, and are usually found, except during the breeding season, in flocks of some six to eight individuals. The flight is labored, with many a quick beat of the wings; but, it is direct and fairly rapid, though seldom sustained beyond some neighbouring tree, where the bird may be seen stealing through the foliage and aiding in its creeping movements with its bill. The most peculiar habit, however, is that of climbing with the whole metatarsus applied to the branch, a fact which adds greatly to its



mouse-like appearance. When roosting, colies are said to pack themselves together in masses, and to hang by the feet; rarely are they seen perching or hopping, though they often cling to the boughs head downwards. Their note is disagreeable and harsh.

The cup-shaped nest of twigs, roots and grass, with a lining of wool or fine grasses, is placed in thick bushes or near the ground in low trees. The three or four eggs, hardly pointed at either end, are dull white or are sometimes streaked with orange and brown.

The food consists almost entirely of fruit, though green shoots, or even insects, are believed to be occasionally eaten.

The eight or nine species of the single genus Colius, ranging through the whole of the Ethiopian region except Madagascar, vary in coloration from brown with darker vermiculations or bars to grey or ash-colour, the abdomen being buff. Fine crests adorn the birds. The sexes are similar, nor are the young very different. The length is from eleven to fourteen inches, due of course to the long tail. (Cambridge Nat. Hist. 1909)

"Colius s. mombassicus (v.S.) is very nearly of a uniform brown color. It is a highly successful Savanna bird, exclusively frugivorous, found over most of the Ethiopian region up to altitudes of about 7,000 feet and







is very numerous in forest clearings. The bird was chosen for study because the gonad-moult cycle was apparently peculiar (Lynes 1934; Moreau 1936), an indication fully confirmed by this present series. The bird has no actual song. Evidence from nests, indicates that its egg laying at Amani is practically confined to the period October-January inclusive, though a little may occur in February." (Moreau, unpublished notes).

Pycnonotus tricolor micrus Oberholser is a member of the family Pycnonotidae, popularly known as bulbuls. The bulbuls have a fairly long bill, usually somewhat stout and curved but may be long and thin as in Phyllastrephus. The wings are normally short, rounded and concave. The tail is sometimes square or graduated, but is commonly rounded, being rarely forked. Crests often occur in the family. Most of the family are characterized by long, fluffy, rump-plumage and conspicuous nuchal or dorsal hairs. Several species of Pycnonotus possess fleshy eyelids of black, red or grey.

Bulbuls are gregarious, arboreal birds of feeble flight, rarely seen on the ground, where they move with awkward shuffles or short hops. The majority are sociable and frequent gardens, orchards, forest and low jungles; they feed chiefly upon fruit, including berries and seeds, but also to some extent on insects. The ordinary note is



a mellow, cheerful whistle, becoming a pretty song in some Pycnonoti; e.g., the Ceylon and Palestine "Nightingales". Chattering and chirping sounds are, however, often heard, while some habitually utter reiterated, jarring or cracking cries, particularly while roosting in company.

The flimsy, or occasionally bulky, nests of twigs, fibres, grass, moss and cobwebs are placed in low trees, bushes, creepers or bamboo clumps. Usually two to four pinkish white or salmon coloured eggs, with markings of various reds and purples are laid, though some members of the family lay white or greenish eggs with brown streaks or spots.

The usual coloration is olive-green, olive-brown or olive-yellow, commonly with wholly or partially yellow, white, greyish or even orange, rufous and buff underparts. The tail and rump may be rufous, yellow, orange, occasionally barred with black; the wings are often adorned with white and yellow markings. The bill and legs range from brown, black or plumbeous, to coral-red, orange, yellow or whitish. The sexes are usually similar.

From their headquarters in the Indian and Indo-Malay countries, the bulbuls extend to China, Hainan, Formosa and Moluccas, with one genus reaching Japan; they also occupy the whole Ethiopian region, with Madagascar and the neighbouring islands. (Cambridge Nat. Hist. 1909).



"Pycnonotus t. micrus (0), a subspecies of the Black-capped Geelgat or Bulbul, a highly successful bird with a mixed fruit and insect diet, occurs at a range from Northern Uganda to the Cape at altitudes up to 7,000 feet. Characteristically a bird of the Savanna, it readily colonizes land cleared of forest, provided that some nesting site well off the ground is available. Since it is always noisy and has no elaborate song, a singing season cannot be designated for it. Judging entirely from the evidence of occupied nests, egg laying by this species at Amani nearly all takes place between mid-September and the end of January. There is no record of any nesting later than February or earlier than September." (Moreau, unpublished notes).

"Phyllastrephus flavostriatus tenuirostris Fisher and Reichenow, the Yellow-streaked Bulbul, also a member of the Pycnonotidae, is confined to the evergreen forests, usually below 4,000 feet, from Pondolan northwards to about Amani. It is almost entirely insectivorous and nests in the undergrowth five to eight feet above the ground and forages upwards through the "mid-stratum" of the forest. Thus it is subjected to the forest eco-climate, though not in its extreme form, and it inhabits an environment markedly more equal than that of Pycnonotus t.





micrus (O.). At Amani, Phyll. f. tenuirostris (F & R) has an extremely well-marked singing period, with full intensity only between late September and early January; though song is not unknown towards the end of August and as late as the end of February. On a basis of seven years records of singing dates, it appears that from year to year the period of fully intense song may vary in date by about three weeks at either end, but where such a purely subjective estimate is concerned, any attempt at a more precise statement would be illusory. Occupied nests found at Amani all give egg laying dates between the end of October and the middle of January." (Moreau, unpublished notes).

#### FIELD DATA

Amani, Tanganyika, where the specimens for study were collected, is situated at 3,000 feet in the East Usambra Plateau (lat. 5° S.) in a clearing in the Intermediate Evergreen Forest. The area has been described elsewhere in the course of a synecological study (Moreau 1935). However, a brief summary of his description is given below, supplemented by additional data received with the material from Amani.





## Rainfall

"Extended dry seasons are not a feature of the Amani climate. Over the period 1903 to 1931, no month of the year averaged less than 72 mm. (about 3 in.) of rain, and

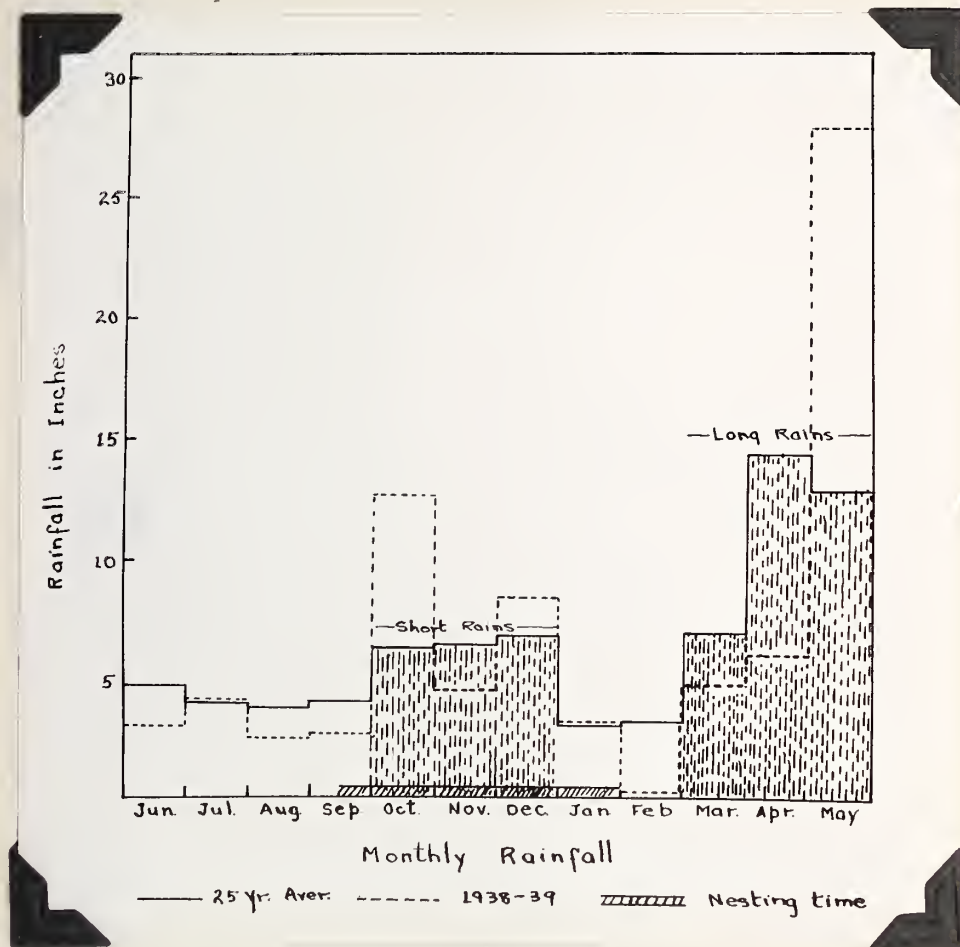


Figure 1

a month with less than an inch was a rarity. However, the rainfall at Amani shows a well-marked peak over the months March-May (the "Long Rains") and a minor one over the months October-December (the "Short Rains"). The mean monthly averages as well as the monthly rainfall during the year



covering the collection of the specimens, are shown in Fig. 1." (Moreau, unpublished notes).

### Temperature and Light

"The annual march of the temperature at Amani is also shown graphically. It will be seen that the three hottest

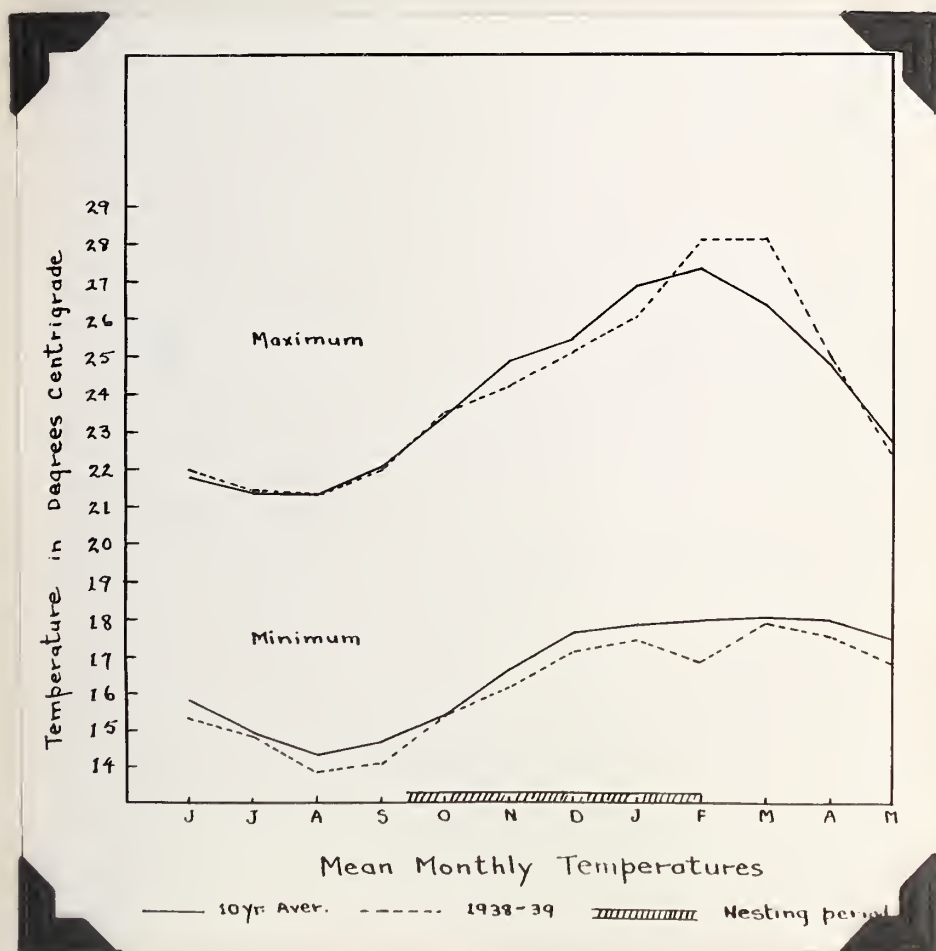


Figure 2

months of the year average about  $4^{\circ}$  C. higher than the coldest. On a ten year average the mean monthly maxima



rise from the June-August figures of  $25.3^{\circ}$  -  $25.7^{\circ}$  C. to the January-March figures of  $26.3^{\circ}$  -  $27.3^{\circ}$  C. and the respective minima from  $14.3^{\circ}$  -  $14.9^{\circ}$  C. to  $17.8^{\circ}$  -  $18.0^{\circ}$  C.

Beneath the forest canopy there is a well marked eco-climate, which probably reaches its extreme development within six feet of the ground. There, apart from actual sun-flecks, the light intensity is between .1 and 1.0 percent of that in the open. The maximum temperatures are about the same as those in the open, but the minimum run about  $3^{\circ}$  C. lower the year round." (Moreau 1935 and Moreau, unpublished notes).

#### Day Length

"The variation in the length of day is 37 minutes in all, from 11 hours 49 minutes to 12 hours 26 minutes. The swing is so low that the day length remains constant for about three weeks at its minimum and again at its maximum. Between 21 June and 1 August it increases only 5 minutes, from 11 hours 49 minutes to 11 hours 54 minutes, and during the months of August and September by 6 and 8 minutes respectively; that is, at the rate of about 15 seconds a day." (Moreau 1936).

#### Humidity

"Atmospheric humidity is high at Amani throughout the year. The annual average of readings at 0900 and 1400



hours has given a relative humidity of 84 percent; the readings were taken in a standard meteorological screen in a large clearing." (Moreau 1936).

#### Summary of Amani Climate

"The Amani climate can be divided into four seasons; the Hot Dry Season of the first quarter of the year, dominated at first by the North-west Monsoon and broken towards the end by frequent thunderstorms; the Long Rains, with steady rain and much mist, trailing off at the beginning of June; the Cool Dry Season of June to September, dominated at first by the South-west Monsoon and often with grey skies; the Short Rains, when the temperature is rising and a few weeks wet weather of very variable type occurs at any time between the beginning of October and the middle of December." (Moreau 1936).

#### LITERATURE

Rowan (1929), in his work on the junco (Junco hyemalis), studied the normal cyclic changes in the gonads in order to have a basis for the comparison of the histological changes in the gonads of his experimental birds. By subjecting the birds to increased periods of light, he





was able to effect recrudescence of the reproductive organs to their maxima, three times within a year. In the junco he found that interstitial cells were present in both the ovary and the testis while the organs were in a state of recrudescence or regression, but were absent in the resting state of the winter testis and if present, were only sparsely represented in the summer. Upon arrival in Alberta in April, the testis of the junco was found to be only in the early stages of recrudescence and even after six weeks there were no free sperms in the tubules. Rowan states that the sperms are probably not liberated till the time of sexual intercourse; but with species that breed in the Arctic, he found that spermatogenesis may be actually completed and sperms found in the tubules while the birds are migrating through Alberta in early May, a month before nesting time in the Arctic. In the junco, he also found that regression was far advanced in the gonads by mid-July, a little over a month after egg-laying time.

Bissonnette (1930), working on the starling (Sturnus vulgaris), published two reports covering the normal yearly histological changes in the testis during the year. He found that the testis, smallest in November and December, enlarged slowly through January, somewhat faster in February and early March, and very rapidly between March 19 and April 1 to a maximum between April 19 to 23. After the breeding season in late April and in May, he found that the



testis underwent rapid regression in June, at rates varying in different individuals. This was shown by the disappearance of the later stages of spermatogenesis from the seminiferous tubules, in reverse order of their appearance in the progressive part of the cycle. He found interstitial cells in inverse ratio to the degree of spermatogenesis. They were indistinguishable from connective tissue cells at the height of the breeding season and were numerous, with rounded nuclei, when regression was evident in the tubule content. In 1936, the same author published an account of the normal progressive changes in the ovary of the starling from December to April, but this work was found of little use in the study of the ovarian cycles of the tropical species because of the new problems involved.

Watson (1919) studied the cyclic changes in the interstitial tissue of the Greenfinch (Ligurnus chloris) and found that there was a decrease in the number of interstitial cells during the active period.

However, literature on the breeding cycles of tropical birds is very scanty. Only in recent years has any work been done on the study of the breeding seasons of the various tropical species. Baker (1938, 1939, 1940) has published several reports on the breeding seasons of various tropical and southern hemisphere birds. In his report (1940) he gives a short account of the histological changes in the



testis of Pachycephalia pectoralis (Latham). This apparently is the first histological work done on the gonads of tropical species, but unfortunately only one paragraph is devoted to this microscopic study. Moreau (1936) published an excellent paper on the breeding seasons of birds of East Africa. Rowan and Batrawi (1939) published a short histological account on the gonads of wintering, northern hemisphere migrants in Africa, prior to their departure for the north in the spring.

#### METHODS

From the 163 sets of gonads (testes and ovaries) collected, only 112 prepared slides for microscopic study were available. Unfortunately, the labels containing the catalogued numbers of the specimens were placed on the outer surfaces of the vials, with the result that many of the labels became detached while the specimens were enroute to Edmonton from Africa. A few vials were also broken and in a few others the alcohol had escaped leaving the tissue unfit for sectioning. However, sections from 70 percent of the material were available for histological study.

All the material was collected under Mr. Moreau's own supervision. Complete and accurate field notes accompanied





the gonads. As Mr. Moreau worked out the yearly moult cycle from these same birds there could be no mistaken identifications in the material sent for study.

It is supposed that all the gonads were fixed in Bouin's immediately after the birds were collected, as the prepared slides showed the material reasonably well fixed. The gonads, upon arrival here, were washed in alcohol, beginning with 70 percent and ending with absolute. They were then embedded in wax and sectioned at 8u and 10u; the ovaries all at 10u. The sections were then stained in Delafield's hematoxylin, cleared in xylol, and mounted in clarite.

Most of the material was suitable for detailed microscopic work with an oil immersion lens.

In order that the histological changes in the testes of the three species might be easily compared, it was decided to make charts representing the progressive changes in each. To do this, brevity was essential; so all descriptions are very short. It is thought that these charts serve the purpose much better than long, tabulated tables or descriptions. Typical sections and others of interest were photographed.

As this is the first extensive histological work on the breeding cycles of tropical birds, an attempt is made to picture the cycles by charts and graphs for comparison with similar works on non-tropical birds. The graphs used to illustrate the monthly changes in the testis are based on a new scheme which presents a clear picture of the actual changes





occurring throughout the year. However, no such graphs could be made to illustrate the female cycles because the ovaries presented several problems which could not be solved from the series under study. It seems that much closer stages, especially during the breeding season, are necessary to eliminate these difficulties.

## TESTIS

### Gross Anatomical Changes

The testes in each of the three species described conform to the general avian type, which has been described by many workers; so no description will be given here.

As is true with non-tropical birds, of which the breeding cycles have been studied (Rowan 1929; Bissonnette 1930, 1936; et al.), the testes and ovaries are smallest midway between two breeding seasons; however, the term "winter condition" cannot be applied to this state of the gonads of tropical forms and so the term "resting condition" will be used instead. This resting period of the testes in each of the three species is very short and occurs mainly during the month of May and the early part of June. From then on there is a gradual increase in size through July and August to their maximum in September in those birds breeding during the



early part of the nesting period. The final stage in spermatogenesis, namely the liberation of free sperms, is probably controlled by some stimulus such as nest building and does not occur in the testis till copulation. This would

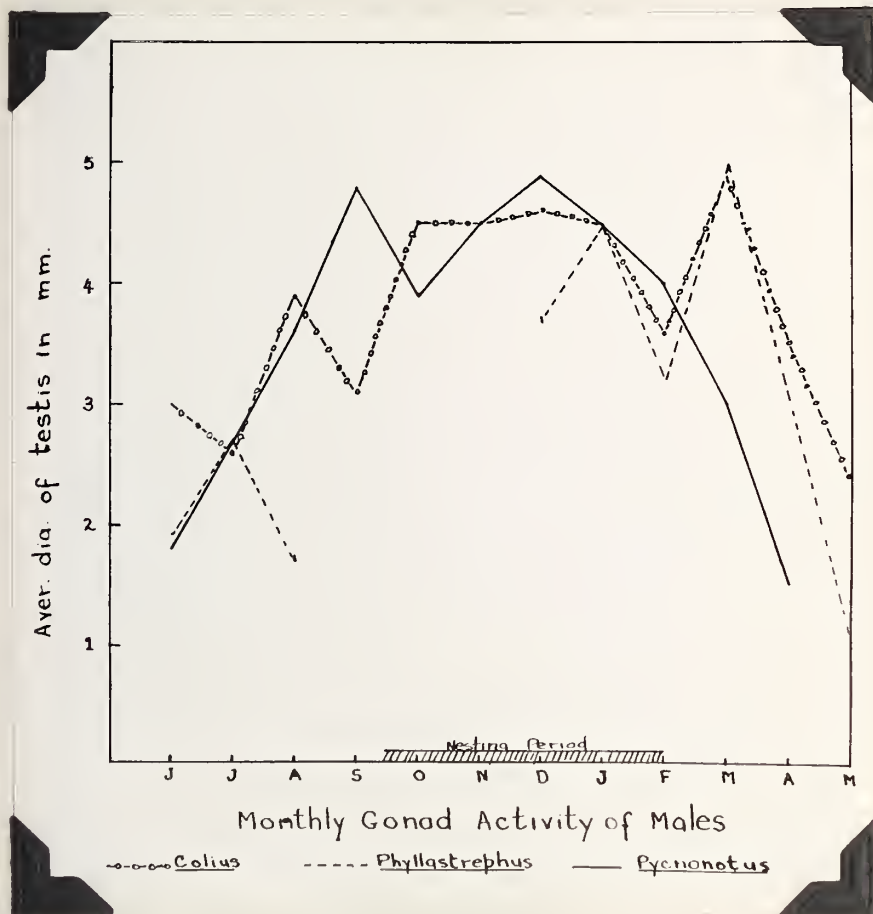


Figure 3

account for the large number of testes, especially in Colius s. mombassicus (v.S.), secured during the prolonged nesting period which had no free sperms in the tubules, but were in near-breeding condition. With these tropical birds, the resting period of the testis is very brief, in contrast to



that of the non-tropical birds studied; whereas, the period of their breeding condition is prolonged, also in contrast to the latter. Moreau (1936) states that the enlargement of the gonads in most Amani birds, including the ones studied here, persist for a much longer time in the males than in the females - nearly four months compared with less than two. A similar relationship obtains among non-tropical forms but the time period, in most species, is much shorter in comparison. However, despite these differences, both the tropical and non-tropical forms have well-marked, yearly breeding cycles.

Testes, in these birds, vary a little in colour with the individual; a few are pigmented, the others not; the pigment is found to be most abundant during the resting stage. In Colius s. mombassicus (v.S.) about one-half the testes contained pigment; in the other two genera, only about one-quarter were found to have pigment. However, only in the smallest testes was the pigment abundant enough to impart a blackish-green colour to the testis.

Pigmented testes in birds are always items of interest to the scientist. From my field-collecting note-book, I find pigmented testes recorded several times for Canadian birds I have collected. Canada Jays (Perisoreus canadensis canadensis) frequently have one testis pigmented and the other unpigmented; other such examples were found in the Horned



Lark (Alpestris otocris hoyti) and in the Pacific Varied Thrush (Ixoreus naevius naevius), but only once in each of the latter two. It is probable, however, that microscopic examination of the unpigmented testes would reveal the presence of some pigment granules in them; but unfortunately none of these specimens were saved for the study.

It may be of interest to mention here that one of the ovarian sections of Colius s. mombassicus (v.S.) showed pigment deposited along the walls of the fallopian tube and also along the outer wall of the kidney nearest it.

#### Microscopical Changes

##### Colius s. mombassicus (v.S.)

A short, descriptive account of each slide from the series covering the yearly breeding cycle is given in the chart on the following page.

Diameter of Testis - From the chart (page 21) and the graph (page 18) it will be seen that the diameter of the testis is of little help in determining accurately the breeding condition of the bird, even though the testis reaches its greatest size during the nesting period and its smallest during the resting period. However, there is too much individual difference in testicular sizes during any





one stage of gonadal development and often testes of equal size are histologically very different. The one may be in the state of recrudescence, the other in regression. (Cf. nos. 77 and 78; 116 and 136).

No.	Month	Largest dia. of Testis in mm.	Pigment	Size of Tubules	True interstitial cells	Interstitial Tissue	Lumen	State of Development
167	Jun-A	3.5	—	quite large	Few	A little	Present	Degenerating Bundles all gone. A few loose sperms
31	Jul-A	2.5	Some	larger	plentiful	"	None	Cell proliferation to 2ndy spermatocyte stage
32	Jul-A	2.8	—	small	None	v. little	"	Cell prob. to early spermatid stage
48	Aug-A	4.4	—	large	v. few	"	Present	Bundles of Mot. sperms. No free sperms
54	Aug-B	3.2	—	small	plentiful	A little	"	Earlier than 48. Bundles just appearing.
55	Sep-A	4.2	Some	large	v. few	v. little	"	Bundles present in a regular row—unlike rest
57	Sep-B	3.7	A little	large	None	"	"	Mostly to spermatid stage. A few bundles appearing.
67	Sep-B	2.4	Some	small	plentiful	plentiful	None	Some cell proliferation, but near resting condition.
73	Oct-A	3.2	quite plentiful	large	A few	v. little	Yes	Similar to 32
77	Oct-B	4.2	—	small	None	"	"	Similar to 48
78	Oct-B	6.2	—	large	"	"	"	Similar to 48
89	Nov-B	4.5	Some	"	v. few	"	"	Similar to 48 but a little earlier
97	Dec-A	5.1	Some	"	None	"	"	Some free sperms
98	Dec-A	4	A little	"	"	"	"	Similar to 97
115	Jan-B	4.1	—	"	v. few	"	Pres	Free sperms quite numerous in a few lumina
116	Jan-B	4.8	—	large	v. few	"	"	Similar to 115
117	Feb-A	3.6	—	"	None	"	"	Early regression. Fewer spermatozoa
136	Mar-A	4.9	—	large	"	"	"	Regression farther advanced than 117
4	Apr-A	3.5	A little	small	plentiful	A little	"	Regression far advanced. Only early stages intact
14	May-A	3.4	—	large	—	v. little	"	Regression farther advanced than 4
159	May-A	2.8	—	small	Rare	A little	None	Approaching resting stage
160	May-A	1.4	Some	small	plentiful	plentiful	"	In full resting condition
161	May-B	2.8	Some	small	v. few	A little	"	Similar to 159
19	May-B	2	Some	small	Few	plentiful	"	Similar to 159
20	May-B	1.9	—	small	plentiful	"	"	Similar to 160

Histological Chart of ♂ Breeding Cycle of *Colius striatus* m.

Under "Month" - A means 1st; B means 15th

Figure 4

Pigment - The pigment, appearing in approximately one-half the sections, is deposited in granules mainly in the connective tissue along the outer walls of the tubules. The reason for the appearance of pigment in some sections and not in others is unknown.



Size of Tubules - The general rule is for the tubules to be smallest in the resting testis and largest in the breeding one; but, here again, there is much individual difference. In some testes the tubules are numerous and small; in others of the same size, the tubules are fewer and larger. (Cf. nos. 48 and 77; 4 and 14).

Interstitial Tissue - A study of the chart shows that interstitial tissue is most abundant in the resting testis and least abundant in the testis in breeding condition; though, here also, individual differences in amounts occur.

Interstitial Cells - Only the true interstitial cells or cell of Ledyig are referred to under this heading. Most of the sections in this series showed interstitial cells and it is probable that all the testes would be found to contain the cells, if they were completely sectioned and all the slides carefully examined with an oil immersion lens. From the slides examined, it appears that these cells are irregular in their time of appearance and abundance throughout the yearly cycle.

State of Development - From the chart, it will be seen that the resting period of the testis is very short, probably six weeks at the most; but the scarcity of material for the month of June makes a definite statement impossible. Recrudescence probably commences in the latter part of June



and the testis may reach its full development by mid-September. Since the nesting season extends over a period of four months, it is likely that the testes remain at or

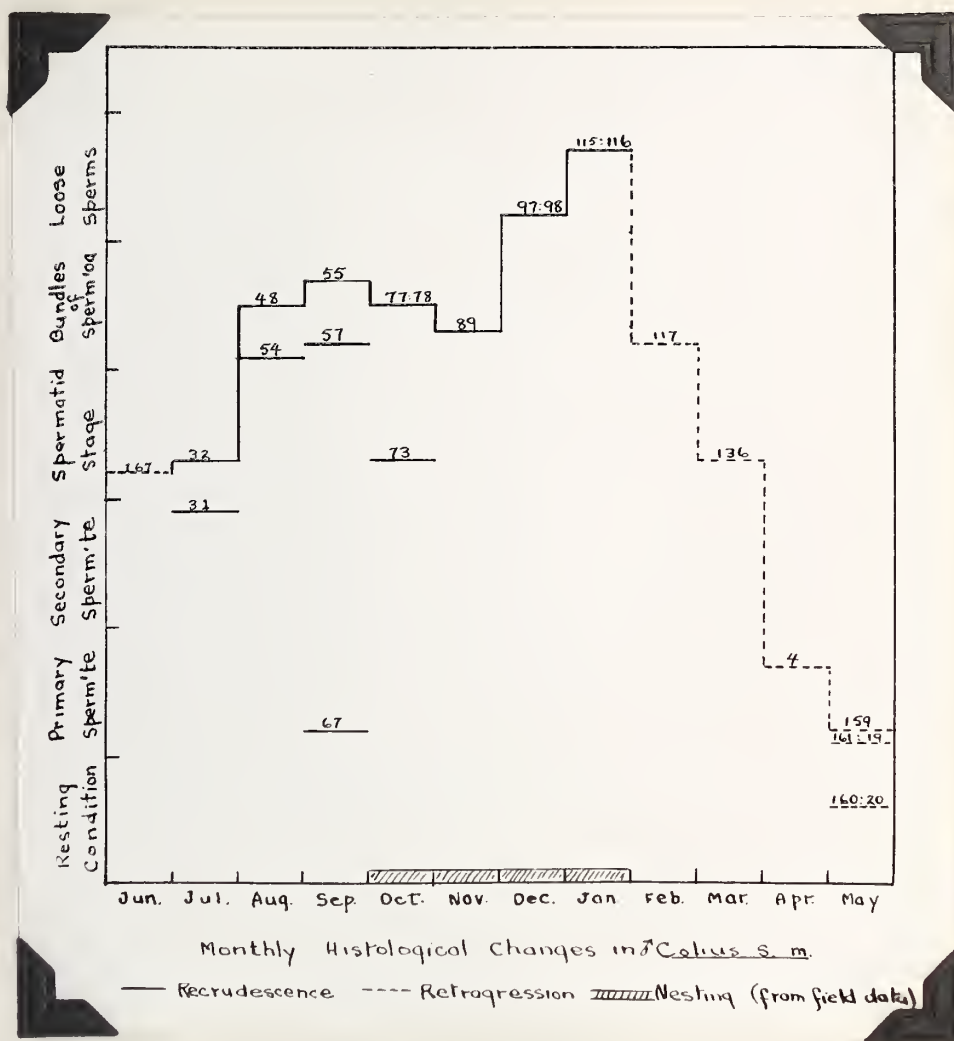


Figure 5

near their height of development during this period. In this series the bundles of spermatozoa are not arranged in a regular row as in most avian testes; instead, their appearance somewhat resembles those of a mammalian testis. There was one exception (no. 55) which contained the bundles in a





regular row like typical avian tissue. Regression commences towards the end of the nesting season, late in January; by May, the testis has reached its resting condition.

Pycnonotus t. micrus (0.)

A short, descriptive chart covering the yearly breeding cycle is given on the next page.

Diameter of the Testis - As with the preceding series, the diameter of the testis may be of little use in deciding the breeding condition of the testis. (Also, see fig. 3, page 18). From the chart, slides 82 and 103 both contain sections of testis from breeding birds; but the former has a section of testis of a diameter of only 3 mm. while the latter has one of 5.5 mm. Normally, a testis with a diameter of only 3 mm. would not be placed with a group of breeding ones. However, the general rule still applies, that the testes are smallest during the resting stage and largest during the breeding period; differences in sizes are attributed to differences in the individual birds.

Pigment - Pigment was found in fewer sections than in the previous series; about one-third of the sections contained some.



Size of Tubules - As is the general rule, tubules increase in size during recrudescence and decrease in size during regression.

No	Month	Largest dia of testis in mm.	Pigment	Size of Tubules	True Interstitial cells	Inter-stitial Tissue	Lumen	State of Development
28	Jun-B	1.9	—	Small	None	A little	NONE	Signs of cell proliferation
35	Jul-A	2.1	—	Quite large	Some	Very little	Present	Bundles of metamorph. sperms appearing
41	Jul-B	2.6	—	Quite small	scarce	Quite plentiful	NONE	Proliferation of cells to secondary spermytestage
53	Aug-B	3.6	—	Medium	V. Few	A little	Pres.	Similar to 35 but a little earlier.
63	Sep-B	4.8	—	large	Quite plentiful	V. little	Pres.	Bundles of sperms no free sperms
75	Oct-B	3.9	some	large	V. few	V. little	large	Mature testis. free sperms in some lumina
81	Nov-A	4.5	some	large	NONE	"	Pres.	similar to 75
92	Nov-A	3	—	large	v. few	"	Pres.	similar to 81
97	Nov-B	3.6	—	quite large	Few	"	PRES.	similar to 92 but very few free sperms
91	Nov-B	4.8	SOME	large	NONE	"	Pres.	Mature. Free sperms abundant
96	Dec-A	3.6	SOME	large	v. few	"	large	similar to 75
103	Dec-B	5.5	—	large	NONE	"	Pres.	similar to 87
108	Jan-A	4.6	—	large	A few	"	Pres.	similar to 91
114	Jan-B	5.2	—	large	A few	"	Pres.	similar to 87
120	Feb-A	3.8	Quite plentiful	large	NONE	"	Pres.	similar to 91
126	Feb-B	4.3	—	large	A few	"	Pres.	similar to 75
134	Mar-A	3	—	Quite small	NONE	some	NONE	Regression far advanced. only early stages intact.
144	Apr-A	2.7	—	Quite small	NONE	V little	Pres.	Mature Testis similar to 126
147	Apr-A	.7	very plentiful	small	plentiful	plentiful	NONE	Nearly in full resting condition
153	Apr-B	1	—	small	"	Some	NONE	In full resting condition
155	May-A	1.4	very plentiful	small	"	plentiful	NONE	similar to 153
166	May-B	1.8	very plentiful	small	—	plentiful	NONE	similar to 153
172	Jun-A	1.7	—	small	NONE	very plentiful	NONE	similar to 153

Histological Chart of ♂ Breeding Cycle of *Bombinus tricolor* m.

Figure 6

Interstitial Tissue - Interstitial tissue is most abundant in the resting testis and least abundant in the testis in breeding condition.

Interstitial Cells - As with *Colius s. mombassicus* (v.S.), true interstitial cells were found throughout the cycle in some sections and were apparently absent in others. They



were most abundant in the testes in resting condition, and in slide 63 they were found to be quite plentiful in a testis approaching full breeding condition.

State of Development - The nesting period of Pycnonotus t.

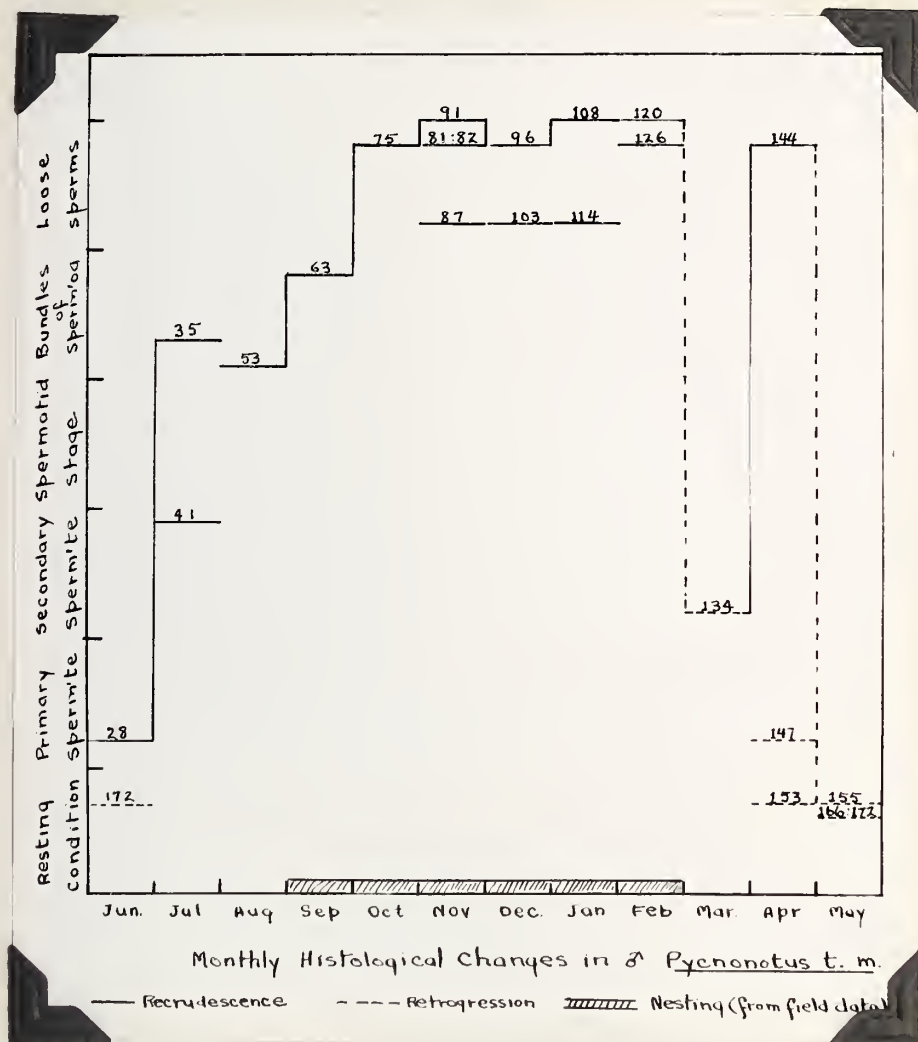


Figure 7

micrus (O.) is the longest of the three species dealt with; evidence from field observations gives the time as early September to late February. Histological study of the testes confirms this (See graph above). The testes are



found in breeding or near-breeding condition from early September to the end of February. Two slides of special interest are to be noted in the chart: slide no. 35 and slide no. 144. The latter contains sections from a testis in breeding condition from the month of April; and the former sections from a testis reaching breeding condition in early July; both were taken from birds collected outside the nesting period. This evidence suggests that nesting may occasionally take place outside the regular period. The resting period of the testis is very short, probably from mid-April to the end of June.

Phyllastrephus f. tenuirostris (F & R)

A short descriptive chart, similar to the previous ones, is given on the following page.

Diameter of Testis - As with the former two series, great differences in size were noted in testes in the same state of development.

Pigment - Pigment was found in only one-quarter of the specimens available for study and probably occurs less frequently in the testis of this species than in the other two.

Size of Tubules - As before, the tubules are largest at the height of spermatogenesis and smallest at its ebb.





Interstitial Tissue - An interesting departure from the general rule is slide no. 11, where very little interstitial tissue is found in a testis in resting condition.

No.	Month	Largest dia. of testis in mm.	Pigment	Size of Tubules	True interstitial cells	Interstitial Tissue	Lumen	State of Development
23	Jun-A	2.3	Some	Small	A Few	A little	None	Recrudescence noted. Primary <sup>1st and 2nd</sup> spermytes quite abund.
26	Jun-B	1.5	—	"	<sup>a</sup> plentiful	<sup>a</sup> plentiful	None	In resting condition. No cell proliferation.
36	Jul-A	2.7	Plentiful	"	?	very plentiful	"	Similar to 26
51	Aug-B	1.7	—	"	<sup>a</sup> plentiful	A little	Appearing	Proliferation of cells to secondary spermyte stage
95	Dec-A	3.7	—	<sup>a</sup> large	"	v. little	Pres.	Breeding condition. Free sperms numerous.
109	Jan-A	4.4	—	large	A Few	"	"	Similar to 95
113	Jan-B	4.6	—	"	<sup>a</sup> plentiful	A little	"	Bundles of sperms. Only a few free sperms
118	Feb-A	1.5	—	Small	v. Few	<sup>a</sup> plentiful	None	In full resting condition
119	Feb-A	5	—	large	<sup>a</sup> plentiful	v. little	Pres.	Like no. 95 — but free sperms not numerous
140	Mar-A	5	—	small	<sup>v</sup> plentiful	v. little	"	Regression far advanced. No sperm bundles.
157	May-A	1.6	—	"	?	Plentiful	None	Abnormal Testis. Much interstitial tissue.
164	May-B	4	—	"	<sup>a</sup> plentiful	"	v. small	In full resting condition
16	May-A	.7	some	<sup>a</sup> small	"	v. little	"	Similar to 164
18	May-B	1.7	—	<sup>a</sup> large	A. Few	A. little	Pres.	Regression far advanced. Similar to 140

Figure 8

Interstitial Cells - In this series, interstitial cells were found to be more numerous than in either of the two previous ones. Again, some testes had numerous interstitial cells, while others appeared to have few if any. It is interesting to note that slides nos. 95, 113, 117 of sections from testes in breeding condition, all had numerous interstitial cells.



State of Development - The nesting period of this species is the shortest of the three, extending from mid-October to mid-January. The histological evidence secured from the micro-

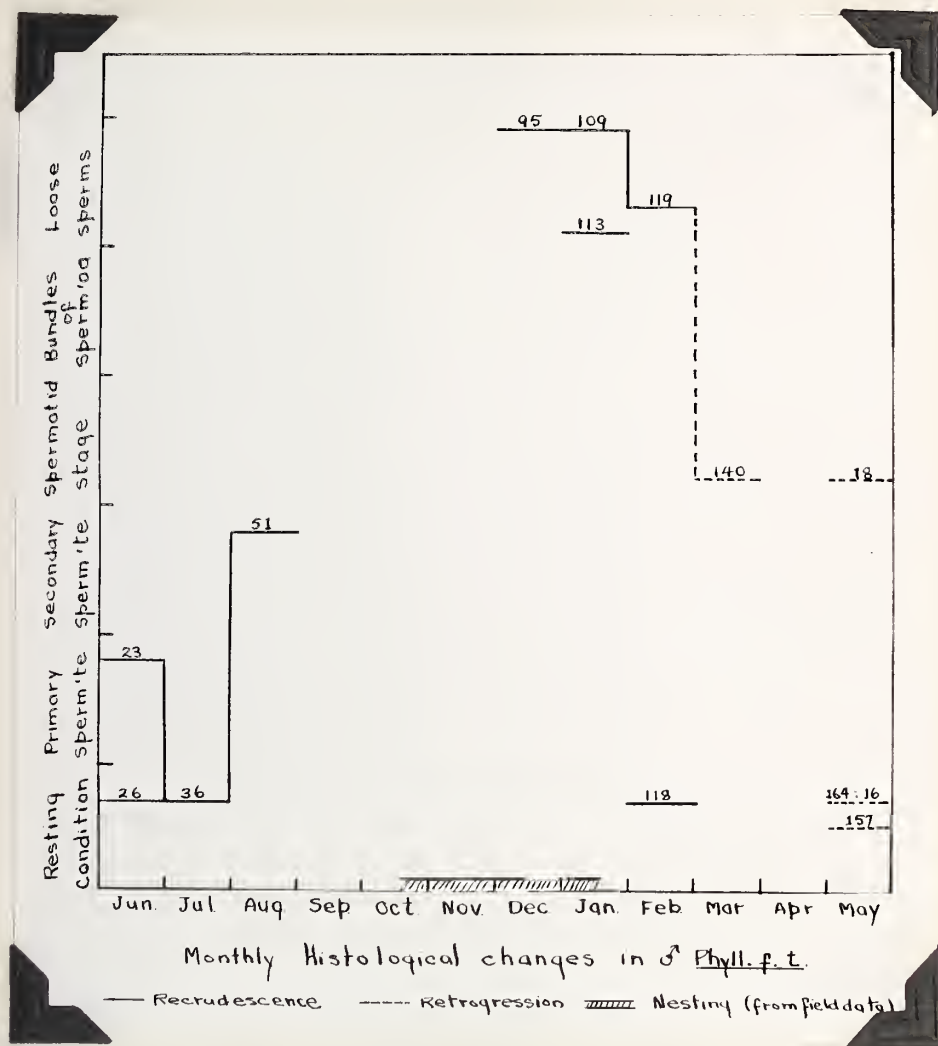


Figure 9

scopic sections seems to confirm this. However, there are no available study specimens for the months of September, October and November. From the trend of the graph it appears that testes in near-breeding condition would have been secured in early October. It also shows that there is a shorter period for testes in full or near-breeding condition,



and a longer one for testes in resting condition; though the scarcity of material in this series makes deductions difficult.

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Tunica Albuginea - The thickness of the tunica albuginea of

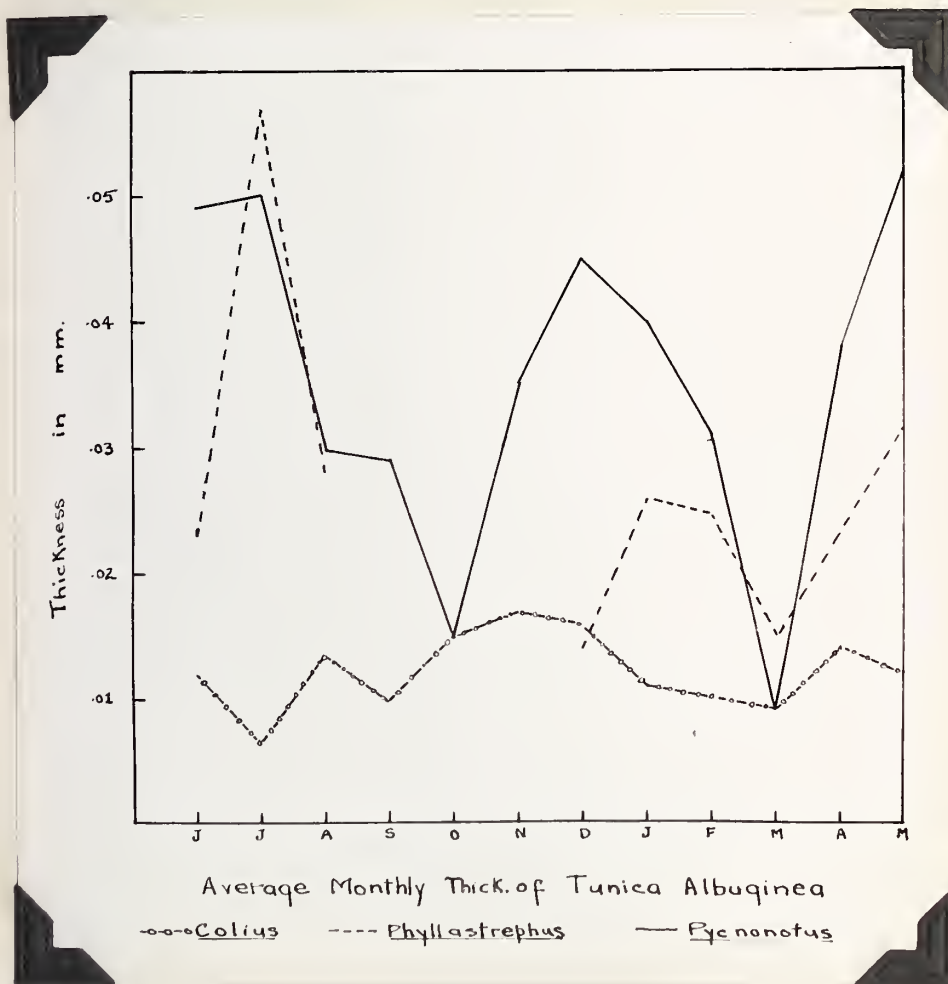


Figure 10

each specimen was measured and the average monthly thickness, for each species, was graphically depicted. The most striking feature of the graph is the line representing the monthly thickness of the tunica albuginea of Colius s.





mombassicus (v.S.), which shows the tunica to be remarkably stable in thickness throughout the cycle. Generally the tunica is much thicker during the resting stage than at any other time. However, the graph shows that there are great individual differences in thickness, especially in Phyllostrephus f. tenuirostris (F & R) and in Pycnonotus t. micrus (O.). In the latter, large testes in breeding condition were found to have thick tunica albuginea. Besides individual differences in the thickness of the tunica albuginea of the testes within the species, apparently there are great differences between species. (See graph).

#### OVARY

Descriptions of the avian ovary are available in many books; a general account seems unnecessary here. With these birds, as with the vast majority of Passeres, only one functional ovary is present.

No attempt was made to weigh the ovaries for comparative purposes, as it would have been impossible to remove properly the small ovaries attached to the kidneys after the material had been fixed. The most advanced follicle in each ovary was measured and the comparative results are illustrated graphically on the next page. From the graph it is seen that very few ovaries in breeding or near-



breeding condition were collected. Since the birds were taken at random at two-week intervals throughout the long nesting period, during which time the individual females would have had different egg-laying dates, it is not surprising

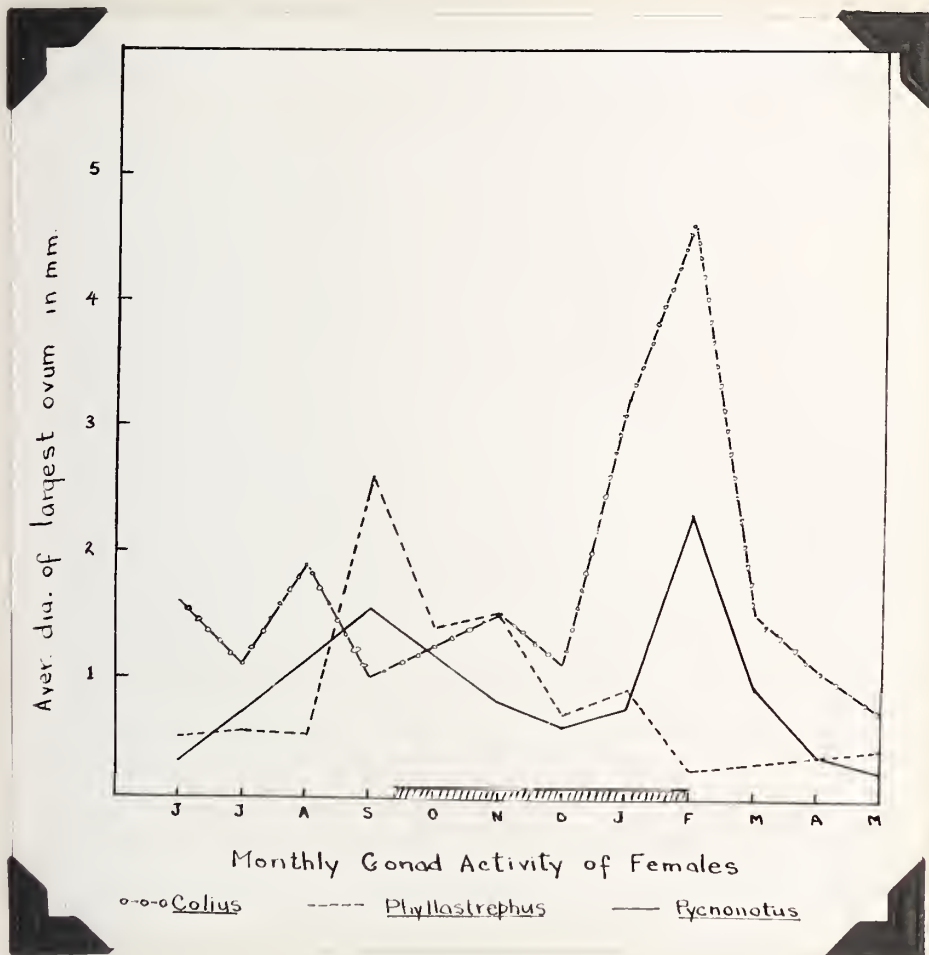


Figure 11

that only a few specimens with greatly enlarged ova were secured. With birds that are gregarious and have a prolonged nesting period, one would have to select his specimens in the field from among nesting birds to secure numbers of individuals with enlarged ovaries; whereas, with birds that



have a short, definite breeding period, all females collected during that period would be in breeding or near-breeding condition. Furthermore, the ovary only enlarges rapidly, through the growth of its follicles, just prior to the laying period of the bird. In the starling, Bissonnette (1936) has shown that this period of rapid rise takes place in the last three weeks prior to ovulation. In the pigeon, Riddle (1911) found that during the last five to eight days before ovulation, the growth rate of the follicles rises to about 8-20 times that formerly prevailing. Similar short periods have been described from various other birds. The period of regression, not as well studied, has probably at its beginning a similar short period, during which there is a rapid decrease in size. Field observations by Moreau and others would seem to verify this assumption, as it has often been remarked that the ovary remains enlarged for a much shorter time than the testis, even in the tropical birds under discussion here. With most birds it is well known that if misfortune befalls the first clutch of eggs, a second is soon forthcoming; but, if the clutch is lost a considerable time after laying, the bird will not lay a second time during the same season. It would seem that if the ovary has regressed past a certain stage it cannot produce any further mature ova during the season. Egg collectors often secure two or three sets of eggs from the same bird by removing the clutch



of eggs as soon as it has been laid; but the second and third sets usually contain fewer eggs.

From evidence secured through field collecting of birds, it appears that the ovary does not remain enlarged for a period much over five or six weeks if the bird is successful in raising its first brood. Thus, with these tropical birds with nesting periods from September to February (note different periods for different species), the problem of deciding the breeding condition of a bird by the histological examination of its ovary is a difficult one.

An attempted solution of the problem by the study of atresia in the ovary throughout the cycle met with little success. It was found that much closer series, than the ones at hand, would be needed for such an undertaking. Furthermore, this study would be less difficult if the work were done on a series of ovaries collected from a non-tropical species with a short, definite nesting period. Atresia in the avian ovary has received little attention. From the study of the ovarian sections of these tropical birds, it appears that atresia is continuously taking place in the ovary, with the possible exception of its resting period in April and May. Evidence of discharged follicles was present in a few sections, but difficulty was encountered in distinguishing the late stages of discharged follicles from those of atretic ones. At least five or





six types of atresia were noted in the different study sections and photographs of several of these are to be found at the back.

## DISCUSSION

Moreau (1936) states, "My data indicate that at Amani on the average (all forest species) the gonads of the individual male remain enlarged for about four months of the year, of the female for less than two." Histological examination confirms this statement as regards the male, but no such conclusive evidence was secured from the study of the ovarian sections because of the different laying dates of the females in such an extended breeding period. But, from the same study, it appears likely that the ovary does not remain enlarged for as long a period as the testis, because only a few enlarged ovaries were collected during the nesting periods.

The seasonal breeding cycles of Amani birds in relation to environmental variants has been discussed by Moreau (1936) in detail and the reader is referred to his work. It may suffice to say that he considers that none of the environmental factors such as light, humidity, rainfall, food-supply or temperature acts as a stimulus or a



limiting factor in the control of these breeding cycles. Nor does he accept the hypothesis of an internal rhythm in the individual as a solution to the problem. He arrives at the conclusion that the observed uniformity and restriction of the breeding season among East African mountain forest avifauna is due to a variety of congruent causes, both limiting factors and stimuli, external and internal.

Thus the factors governing the breeding cycles among tropical birds present a much more difficult problem for solution than among non-tropical forms. Rowan and numerous other investigators following him have shown that daylight is the primary governing factor controlling the breeding seasons of various birds of the north temperate region. In a species with a definite, short breeding period, characteristic of many of our northern hemisphere birds north of the tropics, such a governing factor is possible; but, in an extended breeding period of four or five months in an area like Amani, it is logical to suppose that no one environmental factor could be the controlling one.

In comparing the breeding cycles of these tropical forms with the studied non-tropical ones, a striking difference is at once noted. In the former the testes remain in breeding or near-breeding condition for a long period and in resting condition for a short one; in the latter the reverse is true. In both, there is a definite yearly breeding cycle. Moreau (1936) lists a few species from



the Amani region that are known to be abnormal in their breeding rhythm. For example, among the forest species, Cryptospiza r. australis has been found nesting in every month of the year; Psolidoprocne h. massaica in every month but two and Turturoena in two separate short seasons. Among those birds nesting in the clearing the year round, he lists Coccopygia m. kilmensis, Amauresthes fringilloides and Prinia m. tenella.

Interstitial cells were not found to be constant in their appearance in the testes; although, throughout the three series they were found in certain testis sections from each month of the year. In Phyllastrephus f. tenuirostris (F & R) interstitial cells were found to be abundant in the testes of some of the breeding or near-breeding birds, which is in opposition to the findings of Bissonnette in the starling and Rowan in the junco. Both Rowan and Bissonnette found the interstitial cells fewest, relatively, when the activity of the germ cells was at its height and the birds most active sexually. However, from the study of the testes of the three African species, no conclusive statement can be made about the occurrence of interstitial cells other than that the cells are irregular in their time of appearance in the testes throughout the breeding cycle.

During the resting stage the testis is characterized by its small size, an abundance of interstitial tissue and small tubules without lumina. Within the tubules there





is usually but one layer of cells with small nuclei and thin walls. These cells are found along the inside of the tubule wall, though occasionally they are shoved inwards because of crowding. Besides these small cells, in some sections larger cells with larger, dark, rounded nuclei are to be found, but as a rule they are not very plentiful. The centre of the tubule is filled with finely granulated material, into which cells from the layer along the wall of the tubule are frequently pushed. The tunica propria of the tubules is surrounded by a layer of connective tissue cells, which is frequently obscured by pigment. In most testes, the tunica albuginea is as thick or thicker than the diameter of the tubules within and contains connective tissue cells with flattened nuclei. In some, the tunica albuginea appears to consist of two layers; in others, but one. Blood vessels frequently enter one of these, usually the inner layer.

The first signs of activity in the testis, in the early stages of recrudescence, is noted in the tubules, where the cells have become more numerous and have scattered somewhat throughout the finely granulated material of the tubule. The larger cells with the large nuclei become more abundant. These cells apparently are the primary spermatocytes making their appearance inside the primary layer of cells composed of spermatogonia and Sertoli cells. Mitotic action within the cells was only infrequently seen.

Progression of recrudescence becomes more evident



from this stage on. Secondary spermatocytes soon make their appearance, to be followed by the spermatids, which in later stages are seen to be undergoing metamorphosis.

Meanwhile the testis has been enlarging and the interstitial tissue has become less plentiful between the greatly enlarged tubules. With the appearance of bundles of spermatozoa, lumina become evident in the tubules. This stage is reached just prior to the nesting period of the bird. Testes from breeding birds show an abundance of free sperms in the lumina. This breeding or near-breeding condition, from the evidence contained in the study sections, is retained from about mid-August to the end of January - depending on the species.

The first sign of regression in the contents of the tubules of the testis is the appearance of fewer spermatozoa within. This early stage is difficult to distinguish from a testis just approaching maturity. However, the early presence of debris along with degenerating sperms soon makes the identification of the regressing testis simple. Later stages are marked by the disappearance of the maturing bundles of spermatozoa - to be followed shortly by the disappearance of the spermatids and spermatocytes in succeeding order. During these regressive changes, the centre of the tubule becomes filled with degenerating cells and cytoplasm.

During the time the above changes are occurring within the tubules the testis is gradually becoming smaller due to the diminution in size of the tubules within. Inter-



stitial tissue becomes more plentiful between the tubules and in the testes containing pigment, the pigment granules become aggregated along the outer walls of the tubules. During regression, as noted above, the later stages of germ cells disappear first, as has also been noted by Bissonnette (1930). Generally speaking, regression begins towards the end of February and is completed by mid-May. However, there is much difference in the state of regression in different testes collected at the same date, because it is likely that the testes of some birds begin to regress earlier than others. As remarked before, with birds that have such a long nesting period, great individual differences will be noted in the condition of the gonads at any one time in the breeding cycle.

#### SUMMARY AND CONCLUSIONS

The gonads of three African species of birds collected at 5° S. lat. were studied microscopically to follow the normal histological changes occurring in them throughout the yearly breeding cycle, and brief references are also made to the environmental factors and their possible effects on these cycles.

The testes, smallest in May and the early part of June, enlarge through the latter part of June and through July and August to reach breeding condition in early September in



Pycnonotus t. micrus (O.), and later in the other two species. This breeding condition, with a few exceptions, is maintained till the end of January and possibly through the greater part of February (depending on the species). Regression sets in during the latter part of February and is completed by the end of April or early in May.

The tunica albuginea was found to be remarkably uniform in size throughout the breeding cycle in Colius s. mombassicus (v.S.) and was found to vary greatly in the other two species.

Interstitial cells were found in the tissue of some testes and were absent in others. In Phyllastrephus f. tenuirostris (F & R) they were quite abundant in the testes of most breeding birds while in the other two species they were relatively scarce during the breeding period. All that may be said about these cells from the present study is that they are irregular in their time of appearance and in abundance.

The ovary, like the testis, is smallest in May and in June and increases in size with the growth of its follicles through the remainder of June and through July and August to reach its maximum development in September in those birds beginning to nest in that month and later in the others. However, due to the long nesting period and the different egg laying dates of the individuals, along with the rapid increase of the ovary prior to laying and its rapid decrease immediately





after, few ovaries were found to be in breeding or near-breeding condition.

An attempt to determine the condition of the ovary through the study of atresia and discharged follicles met with little success.

Evidence secured from the microscopic examination of the gonads suggests that nesting may occasionally take place outside the regular period in Pycnonotus t. micrus (O.); but no such evidence was secured from the study of the gonads of the other two species.

A definite breeding season exists with these tropical birds. There is a short resting period for the gonads and a long breeding one - especially in the testis.

This breeding season does not conform with the wet or dry seasons, long or short days, hot or cool periods, nor with periods in which food is abundant or scarce. This is only a confirmation, through microscopical study of the gonads, of Moreau's conclusions through field observations.

No attempt was made to correlate the breeding and moult cycles, though the latter has been investigated by Moreau and the results are at hand.

The complete histological changes occurring throughout the yearly breeding cycle in the testis has been shown by the use of charts and graphs, which have solved the problem of presenting a clear, brief picture of the changes.



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- - PHOTOMICROGRAPHS - -





## TESTES

In photographing the microscopic sections of the testis, it was decided to photograph those illustrating typical stages of recrudescence and regression. However, two of these, namely the resting stage and the early stage of retrogression, are missing from the series because the photographic plates were ruined by light. Other prints were also fogged by light leakage. Unfortunately, those ruined could not be retaken as no extra plates were available. These resting stages are essentially similar to other avian testes in the same condition which have frequently been photographed and illustrated by other workers.

The microscopic sections of the testes of Phyllastrephus f. tenuirostris (F & R) and Pycnonotus t. micrus (O.) are essentially alike, while those of Colius s. mombassicus (v.S.) are very different. (One of the Colius series (no. 55) resembles those of Phyllastrephus or Pycnonotus and it is assumed that the specimen was accidentally placed in the wrong series when the bird was taken.)



Figure 12



No.96

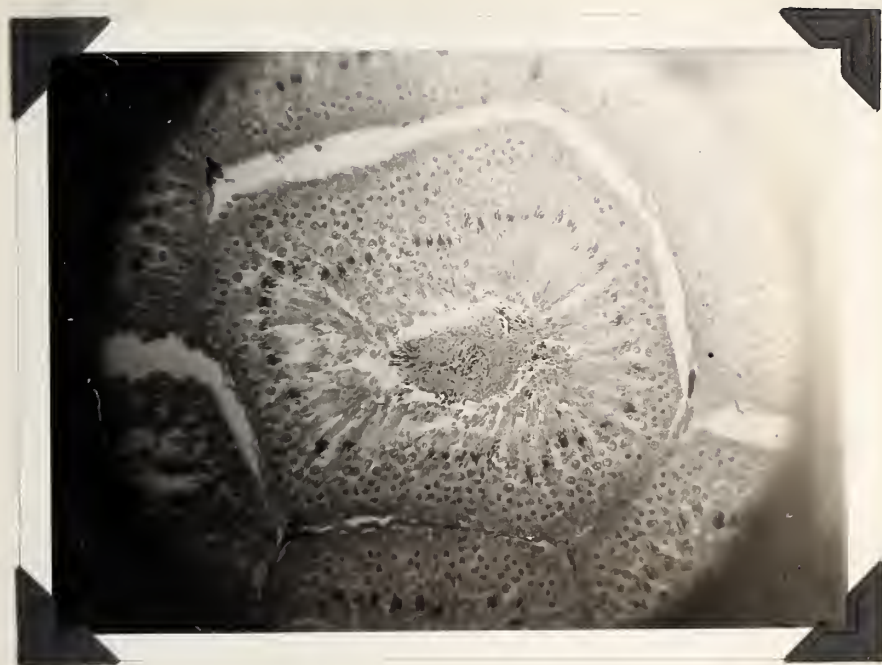
Pycnonotus  
Dec. A

x 42

Although no free sperms are evident in the tubules, some were seen in tubules elsewhere in the section. This section is from a testis in near-breeding condition. Note the regular rows of metamorphosing sperms. At the top are three tubules of the epididymis. Pigment granules are seen along the outer walls of the seminiferous tubules.



Figure 13



No.91

Pycnonotus

x 200

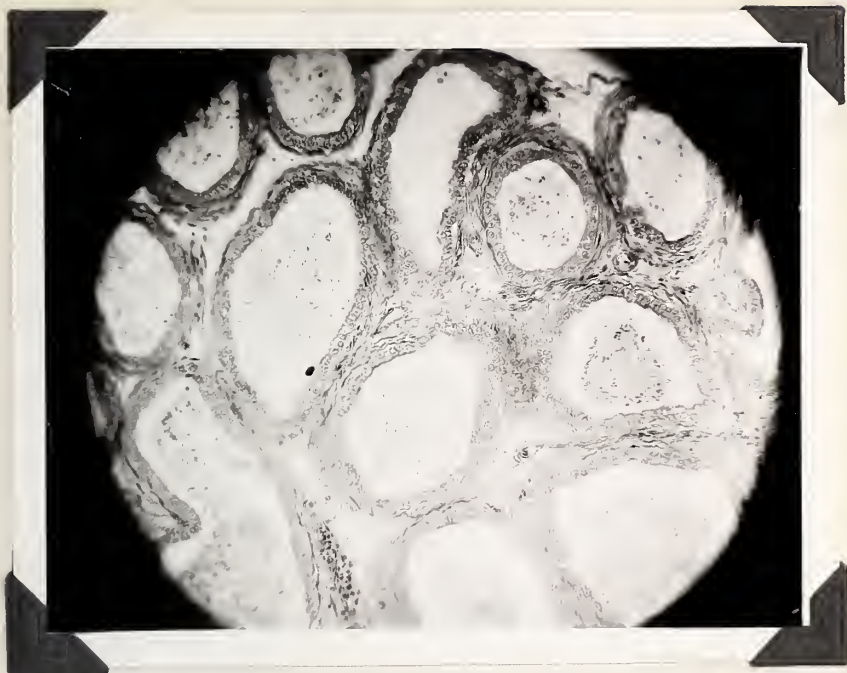
Nov. B

A tubule from a testis in breeding condition. Note the large number of free sperms in the lumen of the tubule and the definite arrangement of the cells in layers from the germ cells to the metamorphosing bundles of sperms.





Figure 14



No.91

Pycnonotus

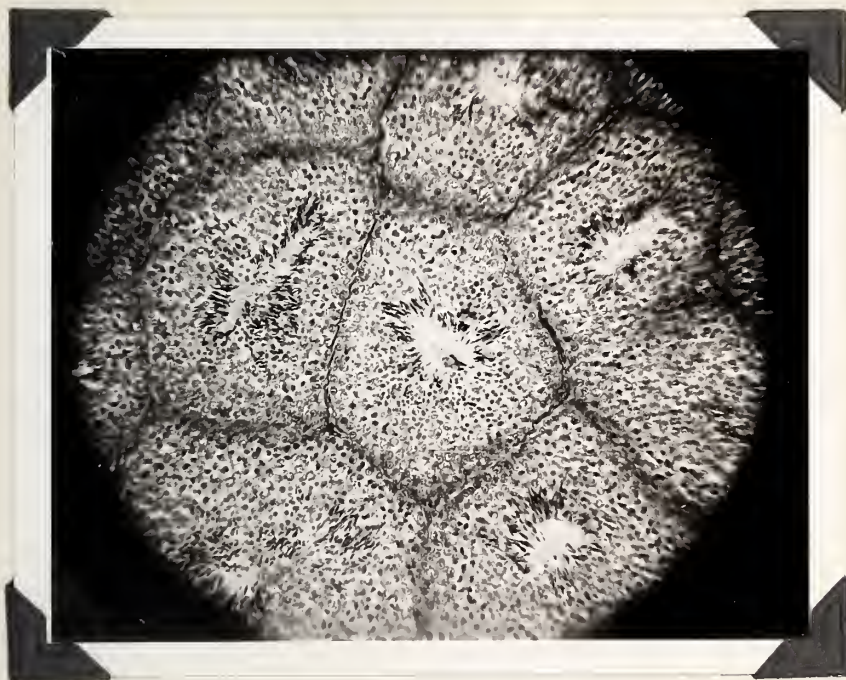
x 200

Nov. B

Photomicrograph of a section of epididymis from the testis shown in Figure 13. Note the glandular cells lining the tubules. The lumina of the tubules are filled with mature sperms as are the tubules of the same testis (Figure 13).



Figure 15



No.115

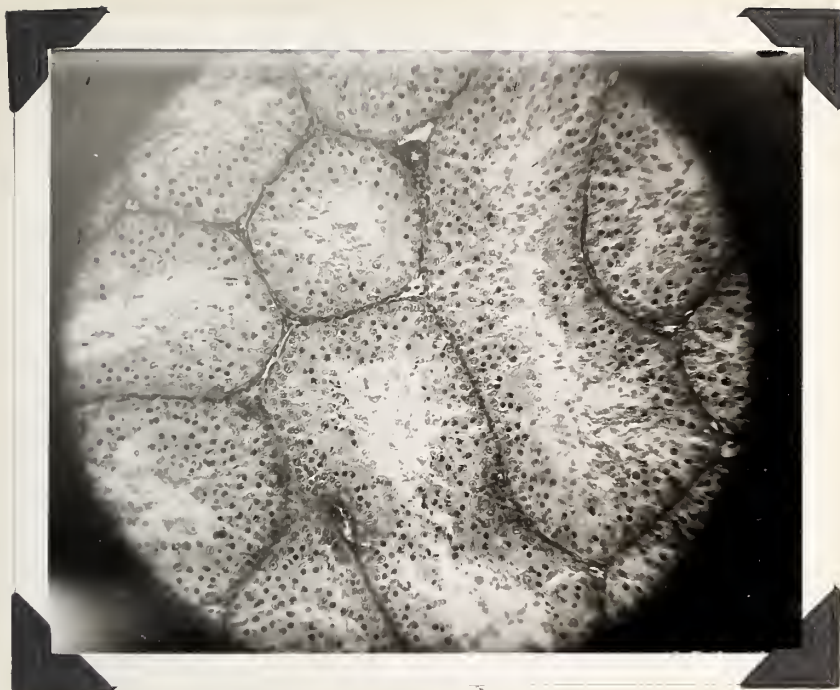
Colius  
Jan. B

x 42

A cross-section of several tubules from a testis of the Colius series showing the different arrangement of the metamorphosing sperms from those of more typical Passerine testes as in Figures 12 and 13. The absence of sperm bundles is the most striking feature of the Colius material.



Figure 16



No. 18

Phyllastrephus  
May B

x 200

Regression is far advanced in the tubules. A few isolated, degenerating sperms are still to be seen but bundles of metamorphosing sperms, spermatids and secondary spermatocytes have all disappeared. Disorganization of the cellular contents is evident; only the early stages are left intact. Debris is seen in the lumina.





## OVARIES

The most striking feature of the ovaries was the presence of countless atretic follicles. These indicate ovarian activity over a large part of the year and suggest a potential breeding season of many months. This condition seems to be in direct contrast to what is known of the ovaries of Passerine species of the Northern Hemisphere.

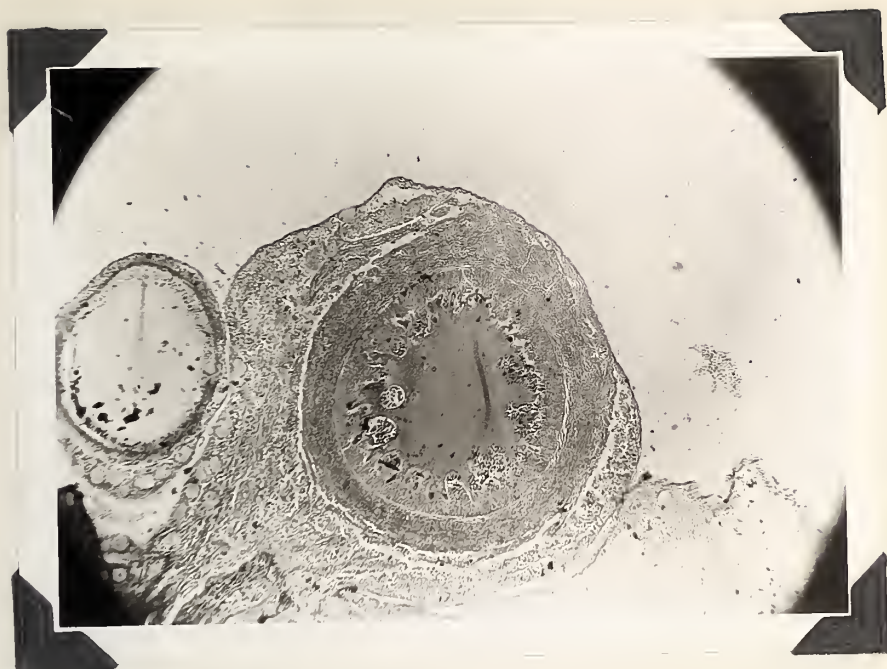
The difficulty, recognized by all the authors who have published anything on atresia in the avian ovary, of distinguishing between atretic and discharged follicles, immediately presented itself and this problem led to a detailed examination of our own material and has resulted in the belief that no certainly discharged follicles are included.

The largest ovary of the series, however (No. 129, *Colius*, Figures 19 and 20), shows three follicles so different from any others (Figure 20) that these might be taken for discharged follicles, but the fact that all these are clustered together is opposed to such a viewpoint. This ovary had two very large yolks (the largest 8.8 mm. in diameter) and the bird was probably laying or ready to lay when collected. In spite of this fact, at least ten large atretic follicles occur on these sections, one of which is illustrated in Figure 19.





Figure 17



No.58

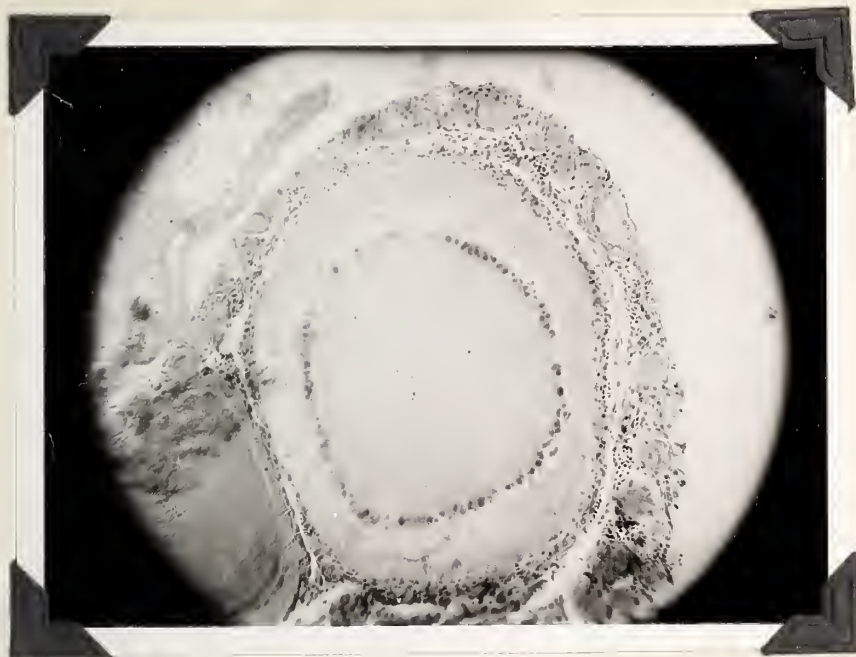
Colius  
May B

x 42

A good example of atresia. Granulosa cells are invading the yolk by proliferation and are forming a cellular outer layer with arms encroaching on inner yolk.



Figure 18



No.169

Phyllastrephus

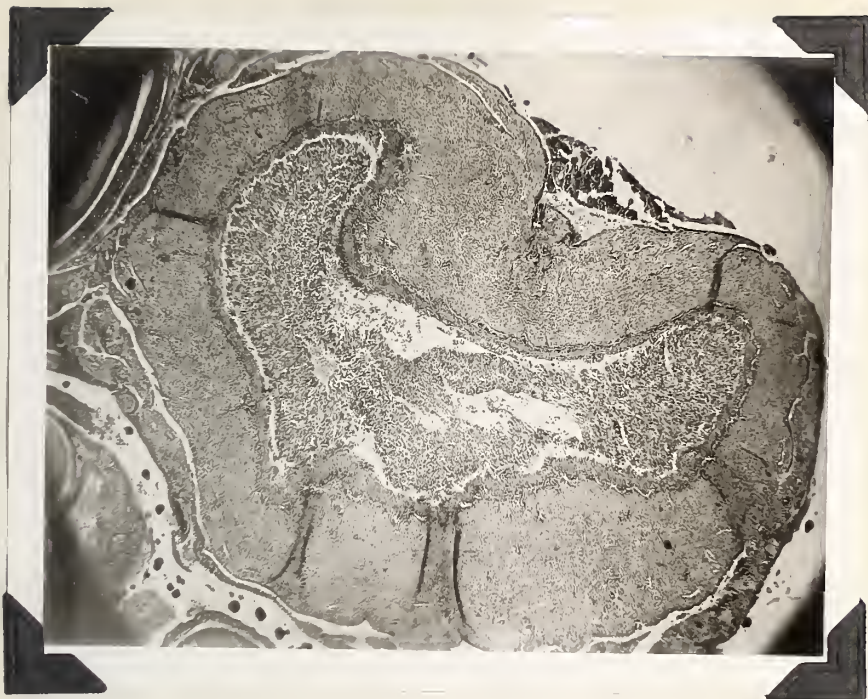
x 42

June A

An atretic follicle in which the granulosa cells appear to have travelled uniformly into the yolk (or the yolk has broken through the granulosa layer and gradually pushed it inwards away from the theca interna). A few other examples of this type have been noted in other sections.



Figure 19



No.129

Colius  
Feb. B

x 42

One of ten similar atretic follicles (this one measured 2.34 x 1.8 mm.) from the ovary which contained several very large ova. One of these (8.8 mm.) was nearly ready to be discharged. A little yolk (y) still remains, surrounded by a mass of small cells of the connective tissue type.





Figure 20



No.129

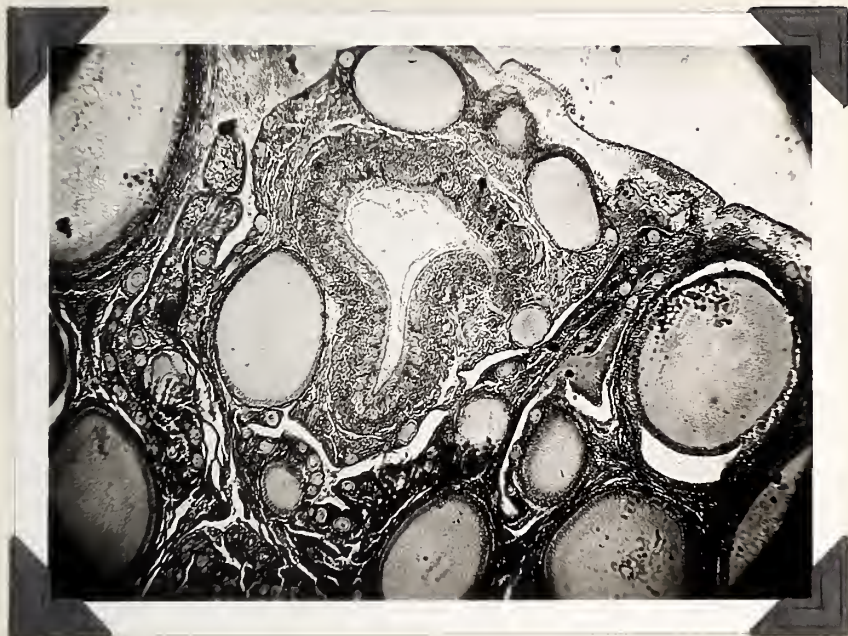
Colius  
Feb. B

x 42

These peculiar looking follicles were found in the large ovary, No. 129. No other ovaries contained anything comparable with these, while this same ovary showed ten of the usual, though exceptionally large, atretic follicles. It is possible that those here illustrated represent discharged ova. This bird was evidently laying when collected.



Figure 21



No.142

Colius

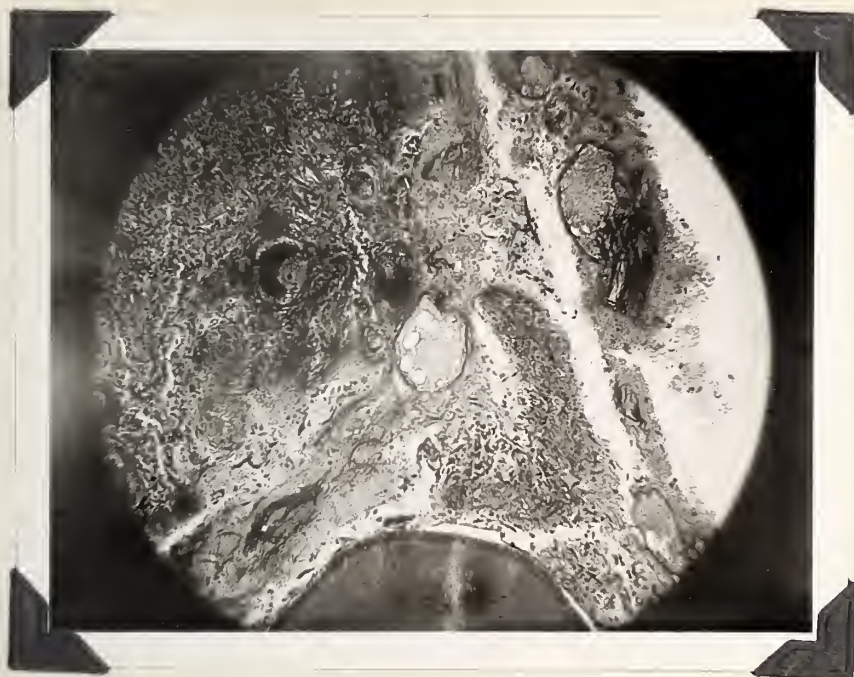
x 42

Mar.13

An atretic follicle with the interior still full of yolk. The granulosa "zone" is seen as a thin layer just outside the yolk. The theca interna contains "nests" of "luteal" cells. (Cf. Pearl & Boring, 1918).



Figure 22



No.170

Phyllastrephus

x 200

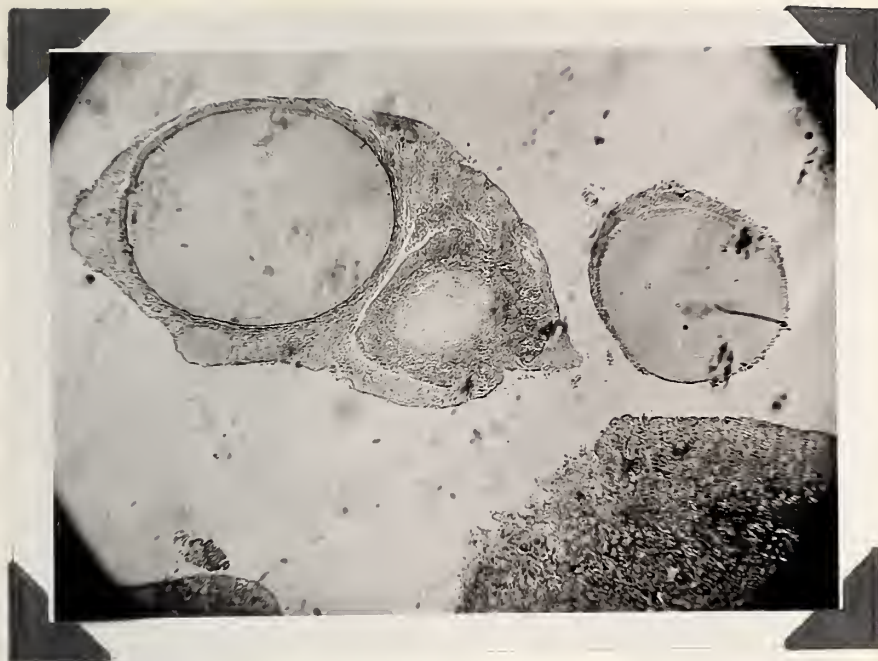
June A

A vacuolated small follicle, evidently atretic (from size) and frequently found in other ovaries. It is distinctly reminiscent of Bramble's "degenerating" ova of sex reversal. (Brambell, 1929).





Figure 23



No.52

Phyllastrephus

x 42

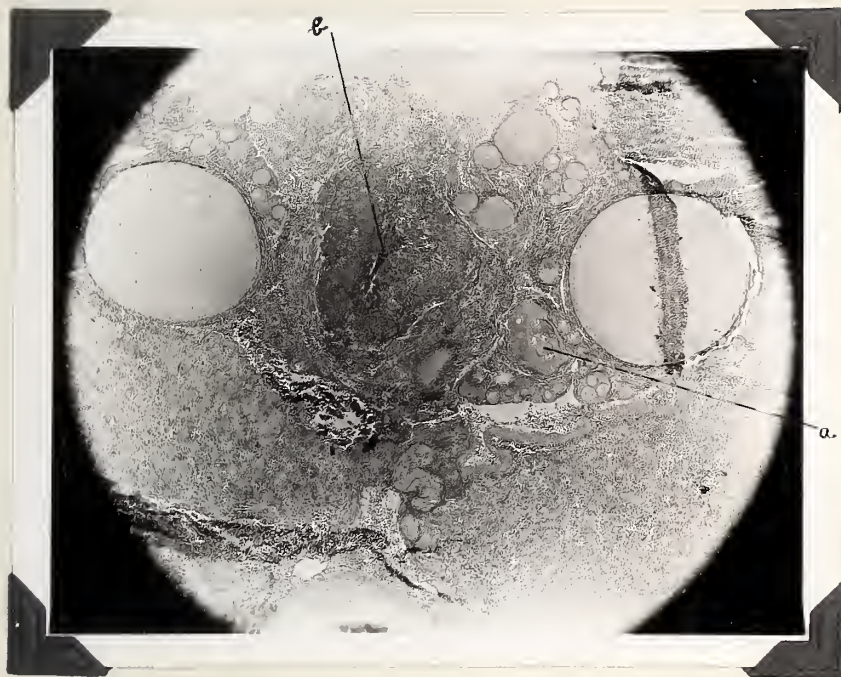
Aug. B

A typical atretic follicle with yolk in the centre. There is an infiltration of cells (granulosa) into the yolk. The theca interna and externa are both still recognizable.





Figure 24



No.124

Phyllastrephus

x 200

Feb. A

The two follicles in the centre are probably both atretic.

(a) The small one certainly is atretic with vacuolated yolk in the centre. It is very similar to No. 170.

(b) The large one, filled mostly with blood corpuscles, may be the last stage of a discharged follicle. The thecal zone is not divisible into internal and external parts.



Figure 25



No.85

Phyllastrephus

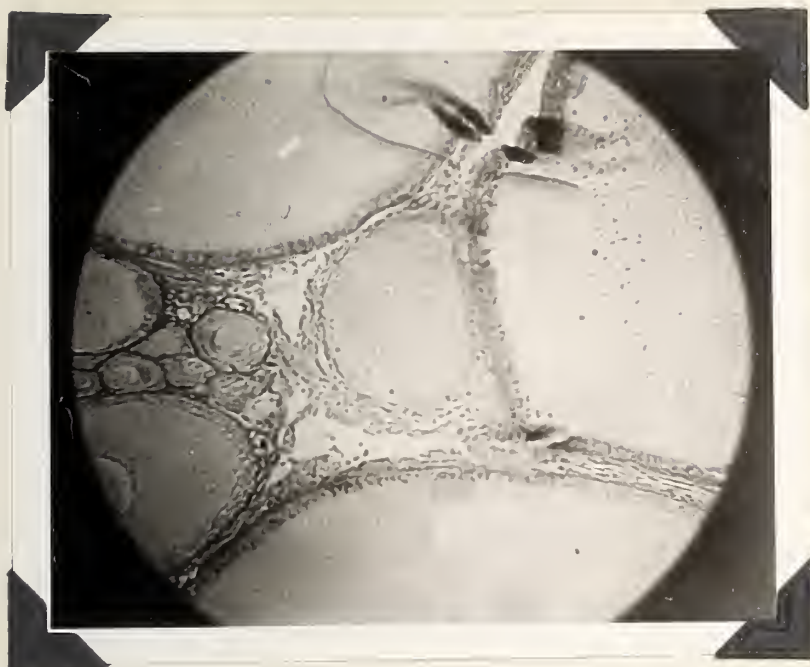
x 42

Nov. A

A typical atretic follicle (a) seen on the margin and an atypical one (b) in the centre. The latter has a fatty appearance with only a few cells recognizable. It appears to consist of connective tissue, interspersed with small blood capillaries.



Figure 26



No.162

Colius

x 200

May B

The central body is completely cellular, although, unfortunately, the cells are not recognizable in the photomicrograph. It is probably a late stage of an atretic follicle. Similar tissue was seen several times in other sections.











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